

## **New large-sized cave-dwelling *Heteropoda* species from Asia, with notes on their relationships (Araneae: Sparassidae: Heteropodinae)**

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**New large-sized cave-dwelling *Heteropoda* species from Asia, with notes on their relationships (Araneae: Sparassidae: Heteropodinae).** - Four new cave-dwelling *Heteropoda* species are described: *H. fischeri* sp. n. from Meghalaya, N India (♂ ♀), *H. schwendingeri* sp. n. from Thailand (♂), *H. beroni* sp. n. from Sulawesi (♂ ♀) and *H. belua* sp. n. from Sarawak (♂ ♀). Notes on the variation and relationships of these species are provided. Additional illustrations and diagnoses are given for the following species: *H. afghana* Roewer, 1962, *H. kuekenthali* Pocock, 1897, *H. nigriventer* Pocock, 1897, *H. robusta* Fage, 1924 and *H. tetrica* Thorell, 1897. The latter species is recorded from Thailand for the first time. Several features found in cave-dwelling species are considered as plesiomorphic for the Heteropodinae (elongated hairs on metatarsus I-III of males) or as convergently developed due to troglobiontic life (large size, elongated appendages).

**Keywords:** Systematics - new species - variation.

### INTRODUCTION

The genus *Heteropoda* Latreille, 1804 is by far the largest genus within the Heteropodinae. More than 180 nominal species were described so far (Platnick, 2004). The genus was intensively revised only with regard to the Australian territory where 38 species are known until now (Davies, 1994). However, as a result of my examination of an exhaustive material of the genus *Heteropoda* I assume that the largest diversity of the genus is present in tropical Southeast Asia (Jäger, 2002, unpubl. data). No comprehensive revision was done so far for Asian representatives. Sethi & Tikader (1988) listed 18 *Heteropoda* species for India and described three species as new (compare the note on *Heteropoda robusta* Fage in this paper and the note in Jäger & Ono, 2000: 45 on *Olios kiranae* Sethi & Tikader). Jäger (2000b) described two new species from Malaysia and Sumatra, Jäger & Ono (2000) one new species from Japan, and Jäger & Barrion (2001) described the male of *Heteropoda cyperusiria* Barrion & Litsinger from the Philippines. Several junior synonyms of the genus *Heteropoda* Latreille and of individual *Heteropoda* spp. were recognized, and some 20 species

were illustrated recently (Jäger, 2002). The recent discovery and description of *Heteropoda maxima* Jäger, the spider with the largest legspan ever found in the world, from caves in Laos (Jäger, 2001a) emphasizes our poor knowledge of this group. In this paper four new large-sized cave-dwelling *Heteropoda* species are described, some of them with almost 250 millimetres legspan. Five additional species are illustrated for comparison.

## MATERIAL AND METHODS

In species diagnoses and descriptions only exceptions from the diagnostic and synapomorphic characters of the subfamily, genus and species groups are listed. For diagnoses and descriptions of family, subfamily and genus, see Jäger (1998, 2001b) and Jäger & Ono (2000). All measurements are in millimetres. Size classes are according to Jäger (2001b: 14), terminology of leg claws after Jäger (2004). Measurements of palps and legs are listed in the following order: Total length (femur, patella, tibia, metatarsus, tarsus). The origin of tegular appendices (i.e. embolus, conductor) is given as clock positions on the left palp in ventral view. In schematic illustrations of internal duct systems of female genitalia the following symbols are used: Open circle = copulatory opening, 'T'-shaped part = glandular region, arrow = fertilisation duct in direction of *uterus externus*. In the illustrations all hairs are omitted (exception Fig. 2), spines on palps are shown. Beside genital characters, which are considered for diagnoses and descriptions and are discussed in Jäger (2000a, 2001b), an additional taxonomic character is presented here: Slit sense organs close to the epigyneal field (compare with Barth, 2001: 40, fig. 1L). Different positions in relation to the epigyneal field may help to distinguish species. The pocket situated dorsal to the median septum of the epigyne is termed 'septal pocket'. The length of the epigyneal field does not include its anterior bands.

Abbreviations. ALE - anterior lateral eyes, AME - anterior median eyes, AW - anterior width of prosoma, CH - clypeus height, DS - dorsal shield of prosoma, FE - femur, MT - metatarsus, OL - opisthosoma length, OS - opisthosoma, OW - opisthosoma width; PA - patella, PH - height of dorsal shield of prosoma, PJ xx - serial number of Sparassidae examined by Peter Jäger, PL - length of dorsal shield of prosoma, PLE - posterior lateral eyes, PME - posterior median eyes, PP - palpus, PW - width of dorsal shield of prosoma, RTA - retrolateral tibial apophysis, TA - tarsus; TI - tibia; I, II, III, IV - leg I etc.

Depositories (with curators). MCZ – Museum of Comparative Zoology, Massachusetts (H. Levy, G. Giribet), MHNG – Muséum d'histoire naturelle, Genève (P. Schwendinger), MNHN – Muséum national d'histoire naturelle, Paris (C. Rollard), MZBJ – Museum Zoologicum Bogoriense, Jakarta (Y.R. Suhardjono), MZLU – Museum of Zoology, Lund University (L. Lundquist), NHM – Natural History Museum, London (P. Hillyard), NMB – Naturhistorisches Museum, Bern (C. Kropf), SMF – Forschungsinstitut Senckenberg, Frankfurt (P. Jäger), ZMS – Zoological Museum, Sofia (P. Beron), ZMUC – Zoological Museum of the University, Copenhagen (N. Scharff).

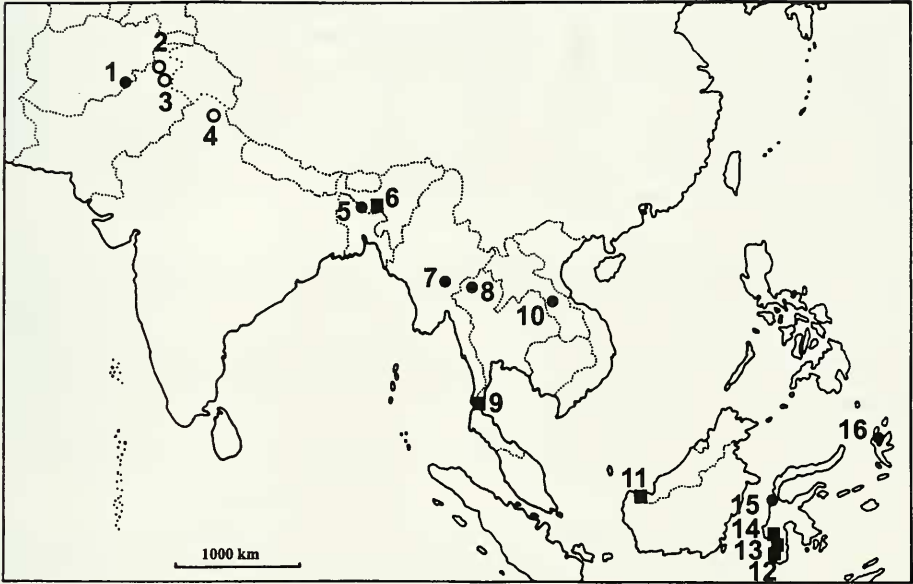


FIG. 1

Records of *Heteropoda* species treated in this paper: 1 Afghanistan, Grotto Tagheh, near Ibrahim Khel (Khouguiani) (*H. afghana* Roewer), 2 Pakistan, Swat, Miandam (*Heteropoda* sp. cf. *afghana* Roewer, PJ 1889), 3 Pakistan, Murree (*Heteropoda* sp. cf. *afghana* Roewer, PJ 407-408), 4 N-India, Kooloo Valley (*Heteropoda* sp. cf. *afghana* Roewer, PJ 222, 386-393, 399-406), 5 N-India, Assam, Garo Hills (*H. robusta* Fage), 6 India, Meghalaya, Jaintia Hills (*H. fischeri* sp. n.), 7 Myanmar, Kayah State (*H. tetrica* Thorell), 8 N-Thailand, Chiang Mai Province, Doi Suthep (*H. tetrica* Thorell), 9 S-Thailand, Chumphon Prov., Nam Lod Yai Cave (*H. schwendingeri* sp. n.), 10 Laos, Khammouane Prov. (*H. maxima* Jäger), 11 Malaysia, Sarawak, Jambusan (*H. belua* sp. n.), 12 Indonesia, Sulawesi, Maros (*H. beroni* sp. n.), 13 Indonesia, Sulawesi, Pangkajene (*H. beroni* sp. n.), 14 Indonesia, Sulawesi, Bone (*H. beroni* sp. n.), 15 Indonesia, Sulawesi, Donggala (*H. nigriventer* Pocock), 16 Indonesia, Halmahera, Soakonora (*H. kueken-thali* Pocock). Filled squares = new species described in this paper; filled circles = known species; open circles = forms with uncertain taxonomic status.

## TAXONOMY

### *Heteropoda* Latreille, 1804

Synonymies and diagnosis: See Jäger (2001b: 19, 2002: 40).

Type species: *Aranea venatoria* Linnaeus, 1767. Designated by Thorell (1870).

*Taxonomic characters.* When looking for valuable characters to group the species described here, one character of the males of almost all these species was very conspicuous: The metatarsi of the second legs have laterally elongated hairs, which are 3.5 to 8.0 as long as the metatarsus width (in few specimens the hairs were rubbed off and only remnants pointed to elongated hairs). In females most of these hairs are only 1 to 1.5 times longer than the width of the metatarsus, only single hairs are longer (2 to 2.5 times metatarsus width). Metatarsal hairs in males appear as a dense and flattened brush (Jäger, 2001: fig. 1E), which consists of lateral scopula hairs and stiff

lateral hairs in the dorsal half of the article. After a more detailed examination of more specimens of further *Heteropoda* spp. and different species from other genera it was clear that 1. elongated hairs occur not only on the second pair of legs, but also - in a less distinct form - on the first and third pair, whereas the fourth pair does not exhibit elongated hairs in comparison to females, and 2. that this sexual dimorphism occurs also in non cave-dwelling Sparassidae i.e. other *Heteropoda* spp., *Sinopoda* spp. and *Pseudopoda* spp., whereas in the latter genus this dimorphism is not very distinct.

The following four forms (*H. afghana*, *Heteropoda* sp. cf. *afghana*, *H. fischeri* sp. n., *H. robusta*) are grouped according to the course of the internal duct system of the female genitalia: 1. Short copulatory ducts, the first semicircular winding of which is directed transversally to body length axis. 2. Glandular structures situated at the end of this first winding (looped apex). 3. Median septum of epigyne clearly visible. 4. Epigyneal field with distinct anterior bands, which may be attached to the field or not. The only known ♂ of this group has a distinct acute appendage on the basal conductor. ♂♂ of other species have to confirm the potential diagnostic relevance of this character for the group.

Note: *Heteropoda lindbergi* Roewer, also described from Afghanistan (Roewer 1962: 8, fig. 87-88) can clearly be excluded from the subfamily Heteropodinae judging from the pictorial and written description of its cheliceral dentition. With two pro-marginal and five retromarginal cheliceral teeth it is most likely a member of the Sparassinae.

### *Heteropoda afghana* Roewer, 1962

Figs 2-11

*Heteropoda afghana* Roewer, 1962: 7-8, figs 85-86.

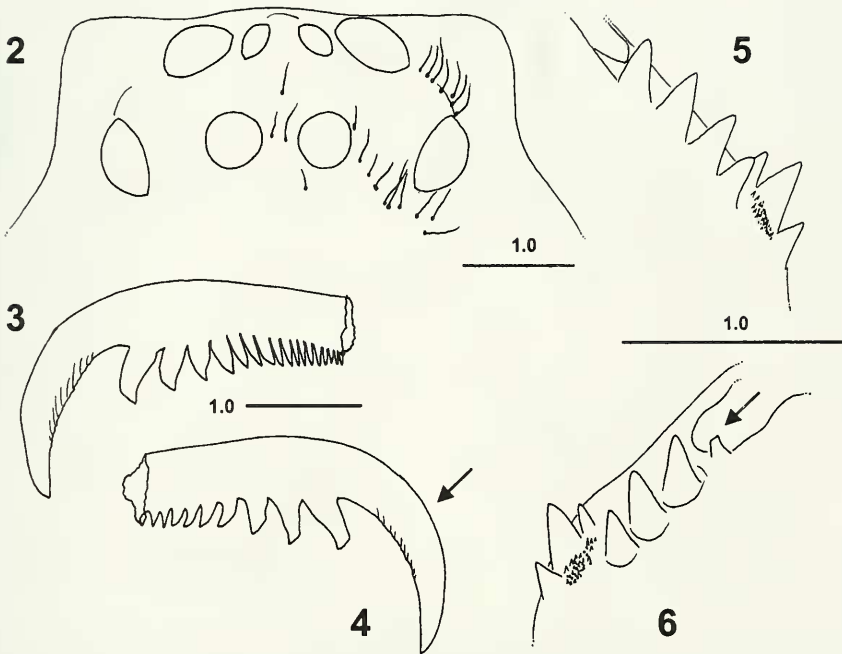
*Material examined*: ♀ holotype (PJ 1887): Afghanistan, Grotte Taghéh Tehinéh, near Ibrahim Khel (Khouguiani), 23.i.1958, Roewer det., Loc. A222, L958/3736, type No. 225:J. (MZLU). *Heteropoda ?afghana*. 1 subadult ♂ (PJ 1888): Afghanistan, Grotte des Tchhel Sotoun, near Djalrez, 20.iii.1958, Roewer det., L58/3353, A212, Kat. 1. (MZLU).

*Diagnosis*: Medium-sized spider with glandular region of internal genital duct system not elevated (Fig. 8, compare with *H. robusta*, Fig. 44), epigyneal field almost as long as wide and with two pairs of relatively large slit sense organs (Fig. 7).

*Redescription* of ♀ holotype (not all measurements could be taken due to the fragile holotype): PL 7.6, PW 7.1, AW 4.0, OL 10.7, OW 5.2. Eyes: AME 0.36, ALE 0.67, PME 0.46, PLE 0.64, AME-AME 0.22, AME-ALE 0.04, PME-PME 0.32, PME-PL 0.57, AME-PME 0.55, ALE-PL 0.60, CH AME 0.70, CH ALE 0.42.

Leg spination: PP 131, 101, 2121, 1014; FE I-II 323, III 333, IV 331; PA I-III 001, IV 100; TI I-II 2026, III-IV 2126; MT I 0004, II 1014, III 2014, IV 3036. Leg measurements: II ? (? , ? , 11.5, 9.6, 2.6), III ? (? , 3.5, 9.1, 7.6, 2.3), IV ? (? , 3.2, 9.5, 9.4, ?). Palpal claw with 6 teeth. Left chelicerae with distal retromarginal tooth distinctly smaller than usual for Heteropodinae (Fig. 6, see arrow). Dorsal shield of prosoma with stiff bristles close to eyes (Fig. 2). Tarsal claws of legs with dominant primary tooth and characteristic shape of distal secondary teeth (Figs 3-4, see arrow). Anterior bands attached to epigyneal field (Fig. 7). For further description see Roewer (1962).





FIGS 2-6

*Heteropoda afghana* Roewer, ♀ holotype. – Eye group, dorsal view (2), bristles omitted in left half; prolateral claw of right leg I, prolateral view (3), base broken off; retrolateral claw of same leg, retrolateral view (4); dominant primary tooth indicated by arrow, base broken off; chelicerae, ventral view, right (5), left (6); distal retromarginal tooth indicated by arrow).

**Distribution:** Only known from the type locality (Fig. 1: 1; see also note on the next form).

**Biology:** The holotype was found in a cave. It cannot be excluded that *H. afghana* represents a troglobiontic species (see also discussion).

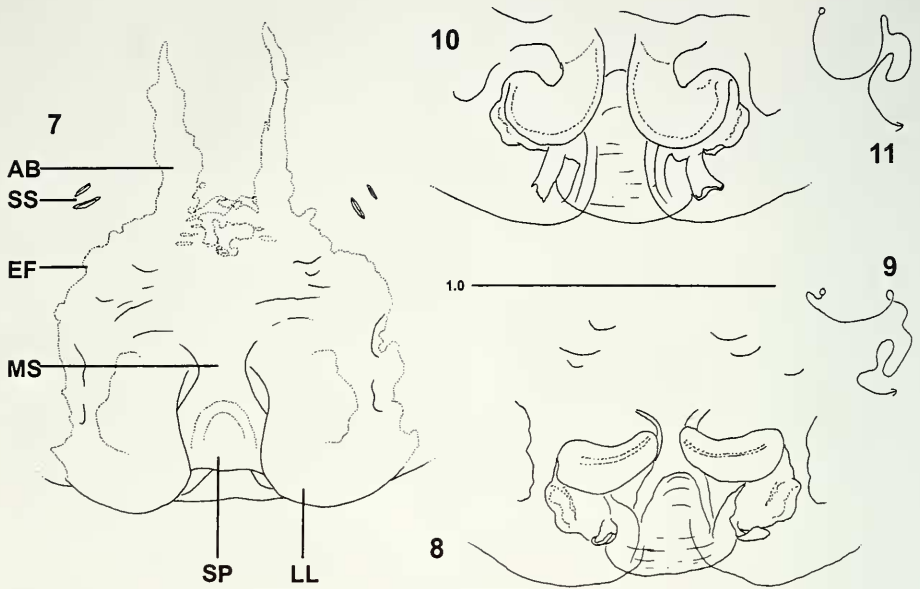
***Heteropoda* sp. cf. *afghana* Roewer, 1962**

Figs 12-28

Material examined: 1 ♀ (PJ 222): North India, Kooloo Valley, Carleton Coll. 8 ♀ (PJ 386-393): North India, Kooloo Valley, ?1874, ?M.M.Carleton. 3 ♀ (PJ 399-401): North India, Kooloo (Valley?), 1876, M.M.Carleton. 3 ♀ (PJ 402-404): North India, Kooloo Valley, 1874, M.M.Carleton. 2 ♀ (PJ 405-406): N. India, Kooloo (Valley?), ?1870's, M.M. Carleton. 2 ♀ (PJ 407-408): Pakistan, Murree, 33°55'N, 73°26'E, 7500ft., 29.vi.1967, Coll. B.L. Haines. (All in MCZ). 1 ♀ (PJ 1889): Pakistan, Swat, Miandam, 1900m, sur la végétation dans un filet d'eau et à la lumière, 17.v.1983, leg. C. Besuchet & I. Löbl (16). (MHNG).

**Variation** (n=20): PL 6.3-11.0, PW 5.8-10.0, OL 8.0-16.3, OW 3.8-10.5. Leg spination (only variation): FE II 333, PA varying from I-IV 001 to I-II 001, III-IV 101, TI II 2126, MT II 0004. Palpal claw with 6 (n=2), 7 (n=17) or 8 (n=1) teeth.

**Note:** ♀ genitalia are similar to those of *H. afghana*, but show the following differences in direct comparison: Anterior bands attached to the epigynal field (Figs 12, 28) or separated (Figs 17, 23, 25). Epigynal field more variable in shape and size.



FIGS 7-11

*Heteropoda afghana* Roewer, ♀ holotype. – Epigyne, ventral view (7); internal genital duct system, dorsal view (8), anterior view (10); schematic course of internal genital duct system, dorsal view (9), anterior view (11). AB = anterior bands of epigyne; EF = epigyneal field; LL = lateral lobes; MS = median septum; SP = septal pocket; SS = slit sensillum.

Distance between septal pocket and epigastric furrow larger. Anterior margins of median septum more strongly bent. Median margins of median septum parallel or at least straighter than in *H. afghana*. Glandular region of internal genital duct system at least in some specimens slightly elevated (Fig. 13). As long as no ♂♂ are known, no further comments on the taxonomic identity of this form can be made.

*Distribution*: N-Pakistan, N-India (Fig. 1: 2-4)

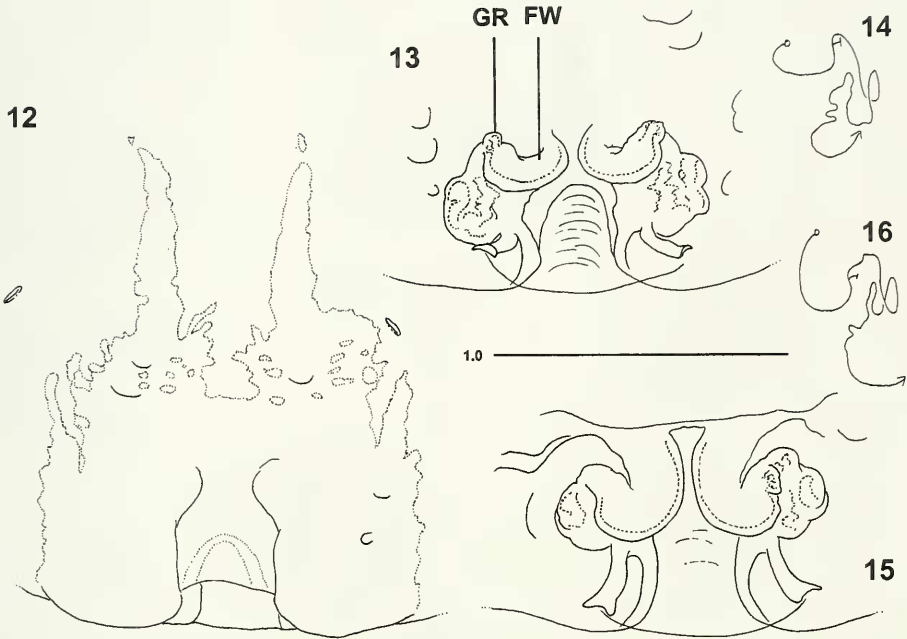
### *Heteropoda fischeri* sp. n.

Figs 29-42

*Material examined*: ♂ holotype (PJ 1756), ♀ paratype (PJ 1757): India, Meghalaya, Jaintia Hills, 'Krem Labbit 2' Cave near Sutnga, N 25°21'59.9", E 92°25'20.6", cave entrance at 1100 m ± 50 metres above sea level, Fischer leg., 25.ii.2001. (SMF). ♂ paratype (PJ 1758), ♀ paratype (PJ 1759): India, Meghalaya, Jaintia Hills, Shnongrim-Area, 'Krem Pyrda' Cave near Ladmyrsiang, N 25°20'30", E 92°29'20", cave entrance at ca. 980 metres above sea level, Fischer & Harris leg. 08.ii.2001. (MHNG). 1 ♀ (PJ 693): India, Meghalaya, Jaintia Hills, Lumshnong-Area, 'Krem Matom' near Mutang, N 25°10'57", E 92°22'01", ± 120m, WGS84, ca. 650 above sea level, 22.ii.1999, Fischer leg. (NMB).

*Etymology*: The specific name is a patronym in honour of the collector Christian Fischer; noun in genitive case.

*Diagnosis*: The species can be generally recognized by its impressive size (23-33 mm body length) and can be distinguished from the closely related and similarly sized *Heteropoda robusta* Fage, 1924 by its genital characters (compare also diagnosis



Figs 12-16

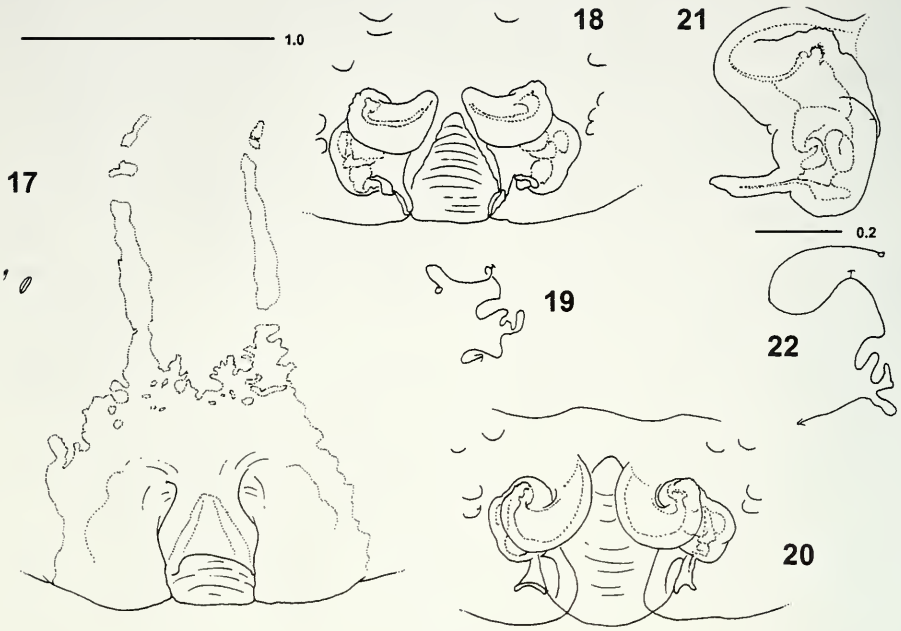
*Heteropoda* sp. cf. *afghana* Roewer, ♀ from Swat, Pakistan (PJ 1889). – Epigyne, ventral view (12); internal genital duct system, dorsal view (13), anterior view (15); schematic course of internal genital duct system, dorsal view (14), anterior view (16). FW = first winding of the internal genital duct system; GR = glandular region.

of *H. robusta* below): ♂♂: 1. Conductor with basal, acute tooth (Fig. 31), 2. Conductor short and compact, 3. Cymbium elongated (Figs 29, 33). ♀♀: 1. Epigyneal field wider than long, 2. Short anterior bands attached to epigyneal field, 3. Visible part of median septum broader than in other species of the group (Figs 35, 38), 4. First winding of the internal genital duct system compact (Figs 37, 39).

*Description:* ♂ (measurements of holotype first, those of paratype in parentheses). PL 12.4 (11.5), PW 11.2 (10.4), AW 5.5 (5.0), PH 2.7 (2.5), OL 15.2 (12.0), OW 9.6 (7.2). Eyes: AME 0.49, ALE 0.77, PME 0.62, PLE 0.79, AME-AME 0.25, AME-ALE 0.04, PME-PME 0.52, PME-PLE 0.57, AME-PME 0.55, ALE-PLE 0.63, CH AME 0.95, CH ALE 0.71.

Leg formula: 2143; spination: PP 131, 101, 2121; FE I-II 323, III 333, IV 331; PA 101; TI I-III 2226, IV 2126; MT I-II 1014, III 2014, IV 3036. Measurements of palps and legs: PP 23.0 (7.9, 3.4, 5.3, -, 6.4), I 96.7 (23.6, 7.8, 27.7, 31.7, 5.9), II 106.5 (26.6, 8.3, 31.2, 34.2, 6.2), III 82.2 (21.2, 7.1, 23.6, 25.1, 5.2), IV 89.7 (23.2, 6.7, 24.6, 29.5, 5.7). Ventral apical spine of MT IV as described for other species of Heteropodinae in Jäger (2001b: 14) here replaced by several bristles. Palp and legs elongated.

Tip of cymbium as long as basal part of cymbium. Embolus arising at 6 to 6.30 o'clock on the tegulum. Sperm duct slightly 'S'-shaped. Conductor stout, not reaching



FIGS 17-22

*Heteropoda* sp. cf. *afghana* Roewer, ♀ from Murree, Pakistan (PJ 407). – Epigyne, ventral view (17); internal genital duct system, dorsal view (18), anterior view (20), lateral view (21); schematic course of internal genital duct system, dorsal view (19), lateral view (22).

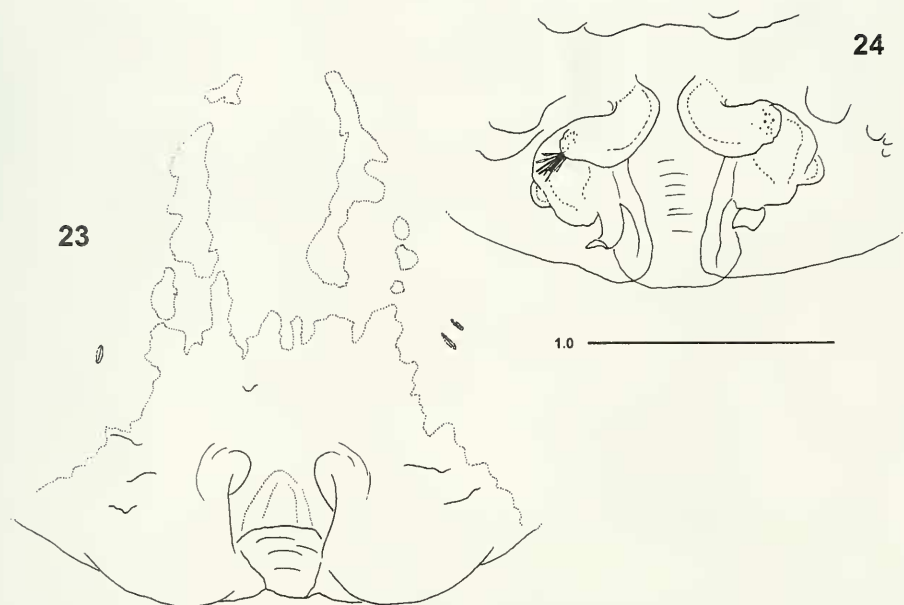
the cymbial margin in ventral view (Figs 29, 33). RTA simple, dorsal part slightly bent and with blunt tip in retrolateral view (Figs 30, 34).

Colour: Yellowish brown, with brown to dark brown markings, these partly consisting of short black hairs. Chelicerae deep reddish brown to black. DS with two dark transversal bands, one in front of fovea and one behind, and additional irregular patches. Head region and margin of DS dark. Gnathocoxae and labium reddish brown, sternum, ventral coxae and trochanter yellowish brown, without pattern. Legs yellowish brown with distal segments darker (i.e. reddish brown). FE with dark spine patches; PA with basal half dark; TI slightly annulated. Dorsal OS with sigillae darkened. A dark transversal bar in the posterior half of OS, behind that a pale brown area. Lateral sides of OS with irregular dark patches. Ventral side of OS yellowish brown, without pattern.

♀ (measurements of paratypes). PL 12.1-14.5, PW 11.0-12.7, AW 6.1-7.2, PH 2.3-3.1, OL 15.6-18.5, OW 9.5-12.2. Eyes: AME 0.56, ALE 0.87, PME 0.64, PLE 0.85, AME-AME 0.40, AME-ALE 0.07, PME-PME 0.64, PME-PLE 0.81, AME-PME 0.71, ALE-PLE 0.80, CH AME 1.23, CH ALE 0.95.

Leg formula: 2143; spination: PP 131, 101, 2121, 1014; FE I-II 323, III 333, IV 331; PA 101; TI I-II 2226, III 22(1)26, IV 2126; MT I-II 1014, III 2014, IV 3036. Palpal claw with 9-10 teeth. Measurements of palps and legs: PP 25.0 (7.5, 3.8, 5.7, -, 8.0), I 85.0 (22.1, 8.3, 24.9, 24.2, 5.5), II 92.9 (25.0, 8.4, 27.9, 26.2, 5.4), III 78.6 (22.0, 7.4, 22.6, 22.1, 4.5), IV 84.4 (23.3, 7.1, 23.5, 25.8, 5.1). Ventral apical spine of MT IV





FIGS 23-24

*Heteropoda* sp. cf. *afghana* Roewer, ♀ from Kulu valley, N-India (PJ 387). – Epigyne, ventral view (23); internal genital duct system, dorsal view (24). Looped apex of right spermathecae with bands of tissue attached to the glandular region.

as described for other species of *Heteropodinae* in Jäger (2001b: 14) here replaced by several bristles. Palp and legs elongated.

Epigyneal field wider than long; anterior bands much shorter than epigyneal field. Internal genital ducts with one anterior winding. Spermathecae situated posterolateral to first winding. Glandular area of internal genital duct system situated in a lateral position on the anterior winding (Figs 35-42).

Colour: As in ♂, but ventral side of OS in one specimen (PJ 1759) darker brown.

*Distribution*: N-India, Meghalaya, Jaintia Hills: Caves near Sutnga, Ladmysiang and Mutang (Fig. 1: 6).

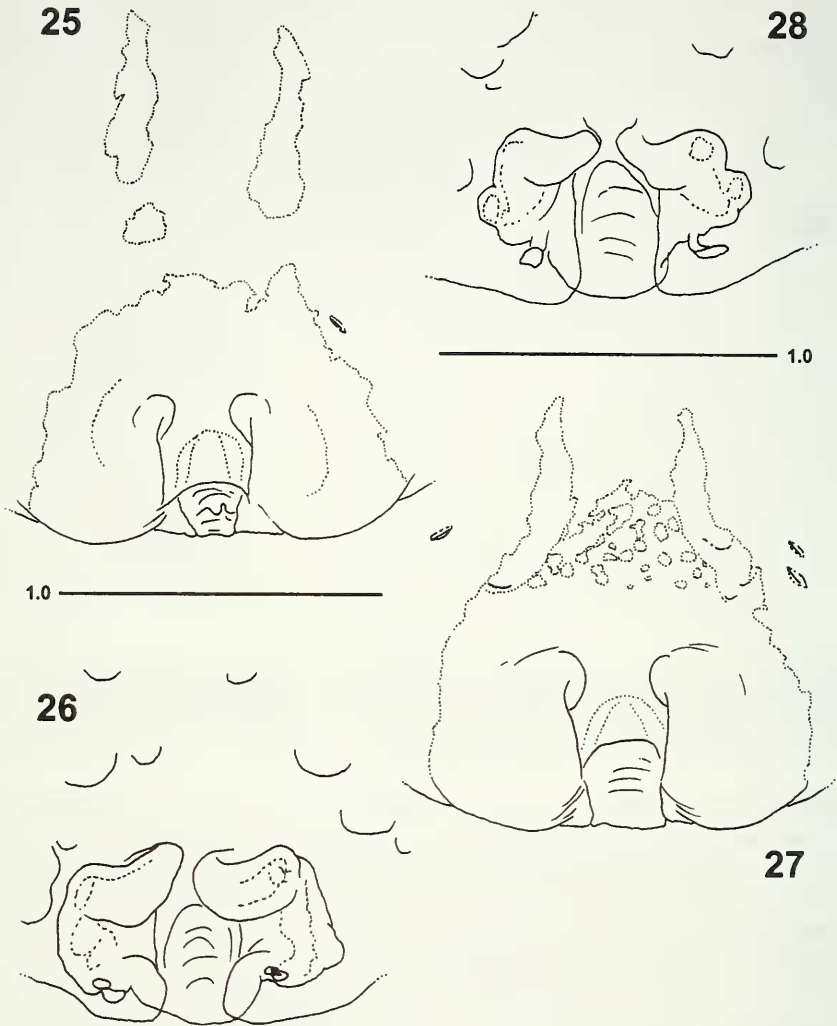
*Biology*: Adult and immature specimens can be found at the same time. All specimens examined were found at the entrance and in the transition area of the cave. Groups of three to eight individuals were observed sitting on the cave walls. Single spiders kept a distance of 30 to 100 centimetres from other spiders. All specimens were perching in the same position, facing downwards and ambushing for prey. As potential prey of *Heteropoda fischeri* sp. n. frogs, scorpions and snakes were observed inside the cave. The body size of the spiders is generally larger the lower the altitude of the cave.

***Heteropoda robusta* Fage, 1924**

Figs 43-45

*Heteropoda robusta* Fage, 1924: 66, fig. 2.

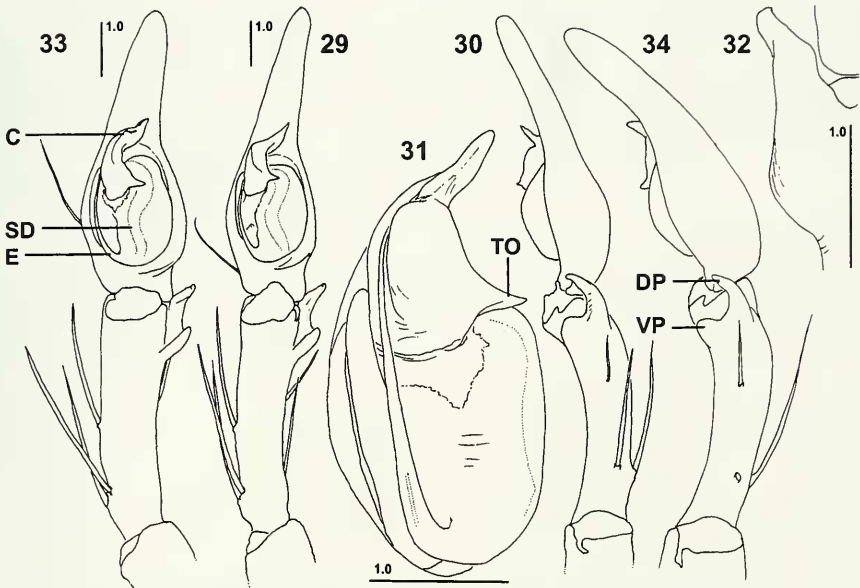
?*Heteropoda robusta*.- Sethi & Tikader, 1988: 10, 17, figs 58-63 (see notes below).



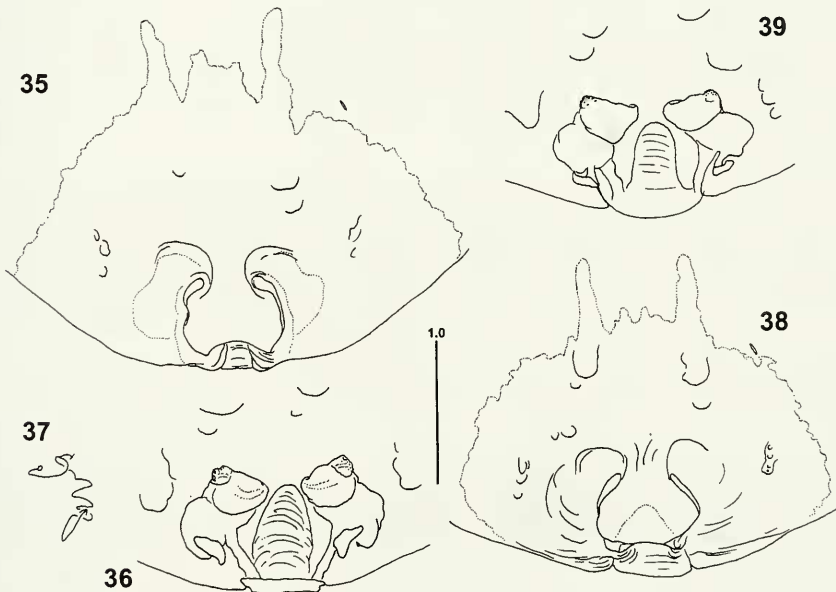
FIGS 25-28

*Heteropoda* sp. cf. *afghana* Roewer, ♀ from Kulu valley, N-India, PJ 222 (25-26), PJ 386 (27-28). – Epigyne, ventral view (25, 27); internal genital duct system, dorsal view (26, 28).

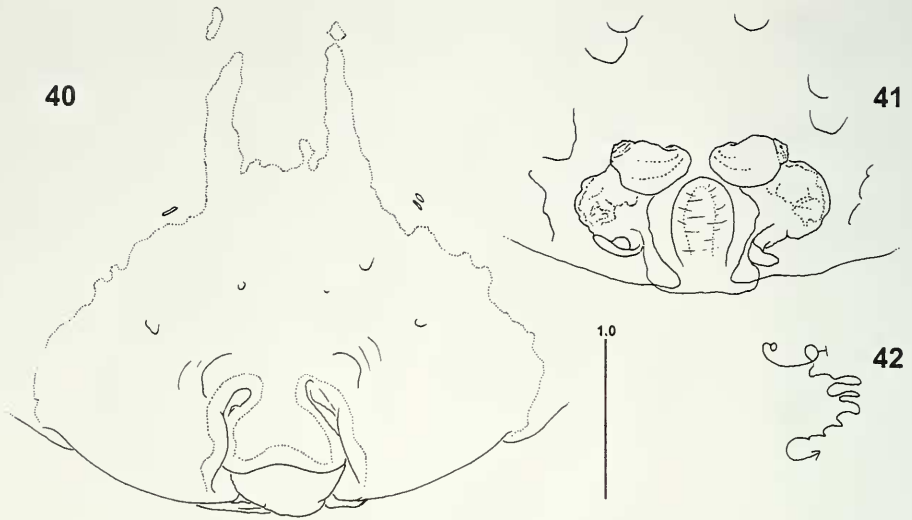
*Material examined*: 1 ♀ syntype (PJ 767): N-India, Assam, Garo Hills, Siju Cave, S.K. & B.N.C, ii.1922, 450-500ft. from entrance, 1734 D. (MNHN). 2 immature syntypes: N-India, Assam, Garo Hills, Siju Cave, S.K. & B.N.C, ii.1922, 350-500 ft. from entrance, 1734 A. (MNHN). 2 immature syntypes: N-India, Assam, Garo Hills, Siju Cave, S.K. & B.N.C, ii.1922, 1000 ft. from entrance, 1734 B. (MNHN). 3 immature syntypes: N-India, Assam, Garo Hills, Siju Cave, S.K. & B.N.C, ii.1922, 2200-2400 ft. from entrance, 1734 C. (MNHN). 3 ♀ syntypes, 6 immature syntypes: N-India, Assam, Garo Hills, Siju Cave, S.K. & B.N.C, ii.1922, 450-500ft. from entrance, 1734 E. (MNHN).



FIGS 29-34. *Heteropoda fischeri* sp. n., ♂ holotype (29-32), ♂ paratype (33-34). – Left palp, ventral view (29, 33), retrolateral view (30, 34); tegulum, prolateral view (31); RTA, dorsal view (32). C = conductor; DP = dorsal part of RTA; E = embolus; SD = sperm duct; TO = basal tooth of conductor; VP = ventral part of RTA.

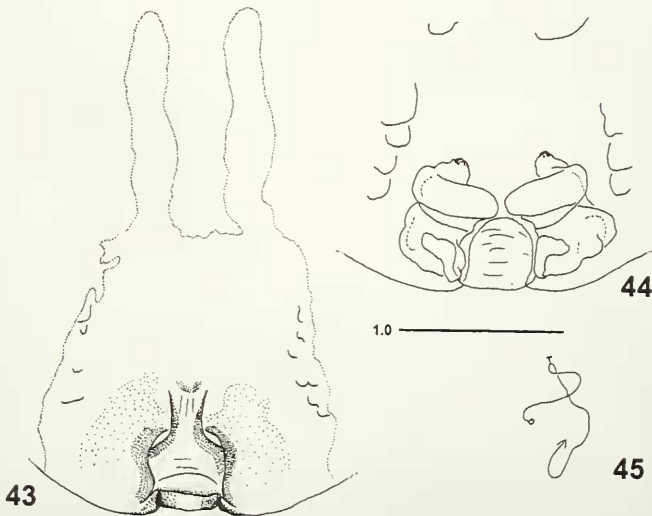


FIGS 35-39. *Heteropoda fischeri* sp. n., 2 ♀ paratypes, from Sutnga, PJ 1757 (35-37), from Ladmyrsiang, PJ 1759 (38-39). – Epigyne, ventral view (35, 38); internal genital duct system, dorsal view (36, 39); schematic course of internal genital duct system, dorsal view (37).



Figs 40-42

*Heteropoda fischeri* sp. n., ♀ from Mutang, PJ 693. – Epigyne, ventral view (40); internal genital duct system, dorsal view (41); schematic course of internal genital duct system, dorsal view (42).



Figs 43-45

*Heteropoda robusta* Fage, ♀ syntype, PJ 767. – Epigyne, ventral view (43); internal genital duct system, dorsal view (44); schematic course of internal genital duct system, dorsal view (45).



*Diagnosis:* Large species (32 mm body length) with elongated appendages (length of second leg 90 mm). ♀♀ may be distinguished from those of the closely related *H. fischeri* sp. n. by their genitalia (Figs 43-45): 1. Epigyneal field slightly longer than wide. 2. Anterior bands almost as long as the epigyneal field. 3. Internal genital ducts similar to those of *H. fischeri* sp. n., but first winding longer. 4. Glandular structures more elevated and situated anterior to the first winding.

*Description:* See Fage (1924).

*Distribution:* Known only from the type locality (Fig. 1: 5; see notes below).

*Biology:* The original description by Fage (1924) gives only few statements on the biology of this species: The spiders were collected from the entrance area to 2,400 feet inside the cave. Apparently the species is abundant in the cave. ♀♀ with egg-sacs and juveniles were found together.

*Notes:* According to the original description by Fage (1924) 22 ♀ syntypes should be present. In the MNHN only 4 ♀ and 13 immatures could be located. According to the labels, all these specimens are considered as belonging to the syntype series. The whereabouts of the 5 missing specimens are unknown.

Sethi & Tikader (1988) described and illustrated ♂ and ♀ of *H. robusta*. Although they illustrated the palp of a ♂, no diagnostic characters are recognizable from that illustration and no such characters are described or mentioned in the text or in the determination key. The palpal cymbium is not elongated as in other troglomorphic cave-dwellers. The illustrations of ♀ genitalia show no correspondence with the examined type material. Sethi & Tikader (1988: 18) stated that the illustrations were made from a ♀ specimen collected in Kanha National Park and compared with an identified specimen from the collection of the Zoological Survey of India in Calcutta (Regd. No. 2105/18). The illustrated female may represent a subadult specimen (compare note on *Olios kiranae* Sethi & Tikader in Jäger & Ono 2000: 45). Therefore I doubt that the illustrated specimens are conspecific with *H. robusta*. Thus the ♂ of this species remains unknown.

### *Heteropoda tetrica* Thorell, 1897

Figs 46-49

For diagnosis, description, type deposition see Jäger (2001b: 22).

*Material examined:* 1 ♂ (PJ 1893), N-Thailand: Doi Suthep near Chiang Mai, 1000 m, 11.i.1959, B. Degenbøl, Pr. 2093A, Journ. 1.7.59, # 287. 1 ♂ (PJ 1894), Doi Suthep, 1100 m, 17.xii.1958, B. Degenbøl, Pr. 2010A, 1.7.59, # 289. 1 ♂ (PJ 1895), Doi Suthep, 1000 m, 27.ix.1958, B. Degenbøl, Pr. 1384A, Journ. 1.7.59, # 297. (all in ZMUC).

*Variation:* PL 8.9-9.1, OL 10.0-10.5.

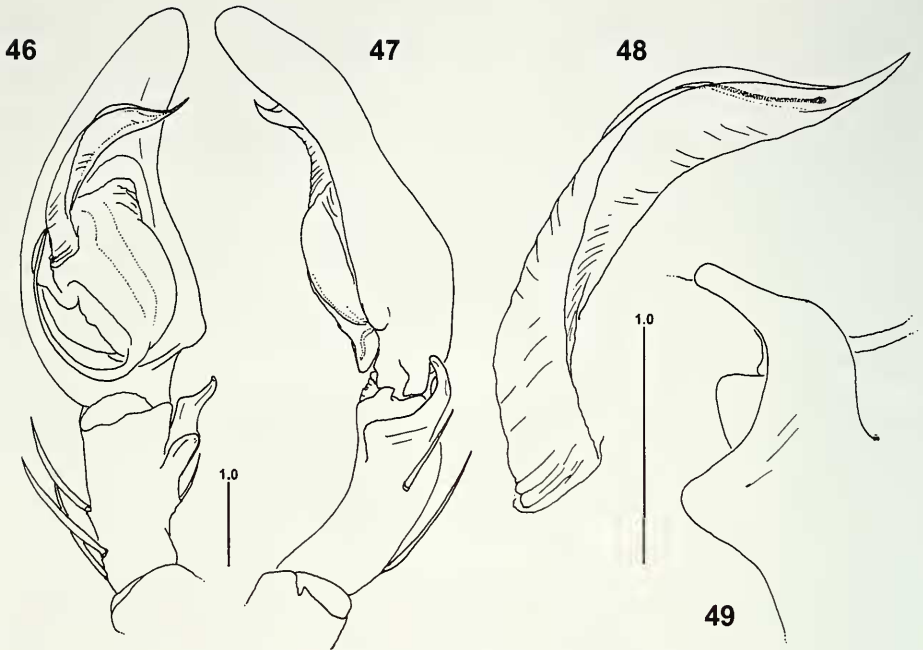
*Distribution:* Myanmar: Kayah State; N-Thailand: Chiang Mai Province: Doi Suthep (Fig. 1: 7-8).

*Note:* The following species (*H. schwendingeri* sp. n.) cannot be grouped with any other species due to the lack of conspecific females. According to male genital characters it could be related to *H. tetrica* Thorell, 1897, which was originally described from Myanmar ('Mons Carin' = Karen Mountains, Kayah State). New records of *H. tetrica* from N-Thailand are listed here for the first time.

### *Heteropoda schwendingeri* sp. n.

Figs 50-58

*Material examined:* ♂ holotype (PJ 1892), Thailand: Chumphon Prov., Nam Lod Yai Cave (=Than Lod Cave), 10°12'58.1" N, 98°56'21.1" E, 100 m, inside limestone cave, 7.v.2003, leg. P. Schwendinger. TH-03/04. (MHNG).



FIGS 46-49

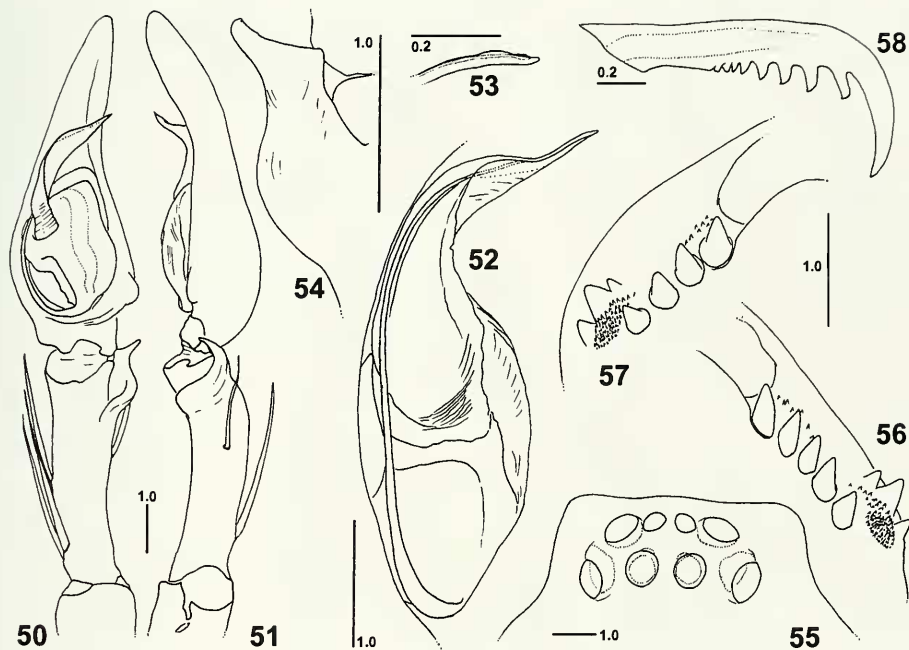
*Heteropoda tetrica* Thorell, ♂ from Doi Suthep, N-Thailand. – Left male palp, ventral view (46), retrolateral view (47); conductor and hidden tip of embolus, ventral view (48); RTA, orthogonal view (49).

**Etymology:** The specific name is a patronym in honour of the collector, Peter Schwendinger; noun in genitive case.

**Diagnosis:** The species seems to be closely related to *Heteropoda tetrica*. It is characterized by its impressive legspan (230 mm) and can be distinguished by male genital characters (Figs 50-54; compare *H. tetrica*: Figs 46-49 and Jäger, 2001b: figs 16a-g): ♂♂: 1. Cymbium elongated (tip of cymbium longer than tegulum), 2. Conductor broad, with sigmoid apical margin, 3. Dorsal RTA with distinct, almost rectangled bulge in dorsal view.

**Description:** ♂. PL 13.3, PW 11.6, AW 5.5, PH 3.2, OL 13.5, OW 7.3. Eyes: AME 0.59, ALE 0.90, PME 0.76, PLE 0.96, AME-AME 0.20, AME-ALE 0.07, PME-PME 0.31, PME-PLE 0.66, AME-PME 0.46, ALE-PLE 0.58, CH AME 1.10, CH ALE 0.90.

Leg formula: 2143; spination: PP 131, 000, 2111, FE I-III 323, IV 331(2), PA I 101, II 10(1)1, III-IV 101, TI 2226, MT I-II 1014, III 2014, IV 3036. Measurements of palps and legs: PP 47.5 (7.9, 3.2, 4.8, -, 7.0), I 97.6 (24.6, 7.8, 29.0, 30.2, 6.0), II 107.8 (27.1, 8.2, 32.1, 34.2, 6.2), III 82.2 (22.4, 7.1, 24.7, 23.3, 4.7), IV 89.7 (24.2, 6.7, 25.9, 5.2, 27.7). Cheliceral furrow with 4 and 5 posterior teeth on right and left side respectively (Figs 56-57). Ventral apical spine of MT IV as described for other species of Heteropodinae in Jäger (2001b: 14) replaced by a brush of bristles. Palp and legs elongated.



FIGS 50-58

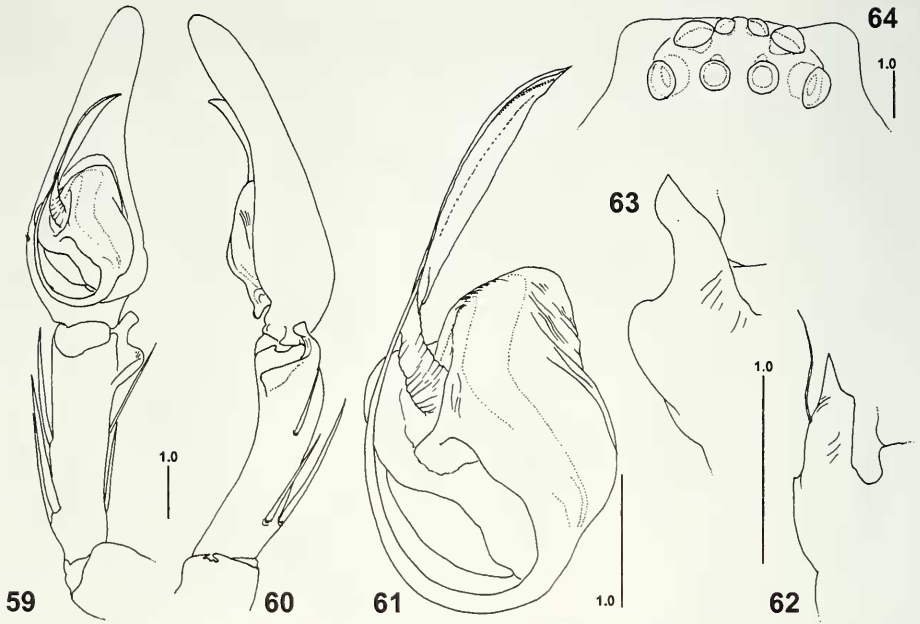
*Heteropoda schwendingeri* sp. n., ♂ holotype. – Left palp, ventral view (50), retrolateral view (51); tegulum, prolateral view (52); tip of embolus, ventral view (53); RTA, dorsal view (54); eye group, dorsal view (55); cheliceral furrow, ventral view, right (56), left (57); retrolateral claw of right leg I, retrolateral view (58).

Embolus arising at 6 o'clock on the tegulum (Fig. 50), its tip simple, with a sub-apical opening of the sperm duct (Fig. 53). Conductor long, reaching the cymbial margin in ventral view (Fig. 50). Sperm duct almost straight. RTA simple in retrolateral view, dorsal part widened in ventral and dorsal view.

Colour: Yellowish brown to light brown, with dark brown markings, these partly consisting of short black hairs. Chelicerae yellowish brown to dark brown. DS with irregular pattern of narrow radial bands and irregular marginal patches. Posterior DS with wide light transversal band. Gnathocoxae and labium light reddish brown, sternum, ventral coxae, trochanter and non-apical FE yellowish brown without pattern, except for indistinctly speckled ventral FE. Legs light brown with distal segments darker (i.e. reddish brown). Spine patches of dorsal FE fused to wide continuous annulations, apical annulation extending around dorsal and ventral side of femur; ventral and prolateral sides of PA with dark basal half; each TI distinctly annulated with two wide bands. Dorsal side of OS with sigillae darkened. Remaining pattern of OS irregular and indistinct. Ventral side of OS brown, without pattern.

♀ unknown.

*Distribution*: Only known from the type locality (Fig. 1: 9).



Figs 59-64

*Heteropoda beroni* sp. n., ♂ holotype. – Left palp, ventral view (59), retrolateral view (60); tegulum, ventral view (61); RTA, dorsal view (62), orthogonal view (63); eye group, dorsal view (64).

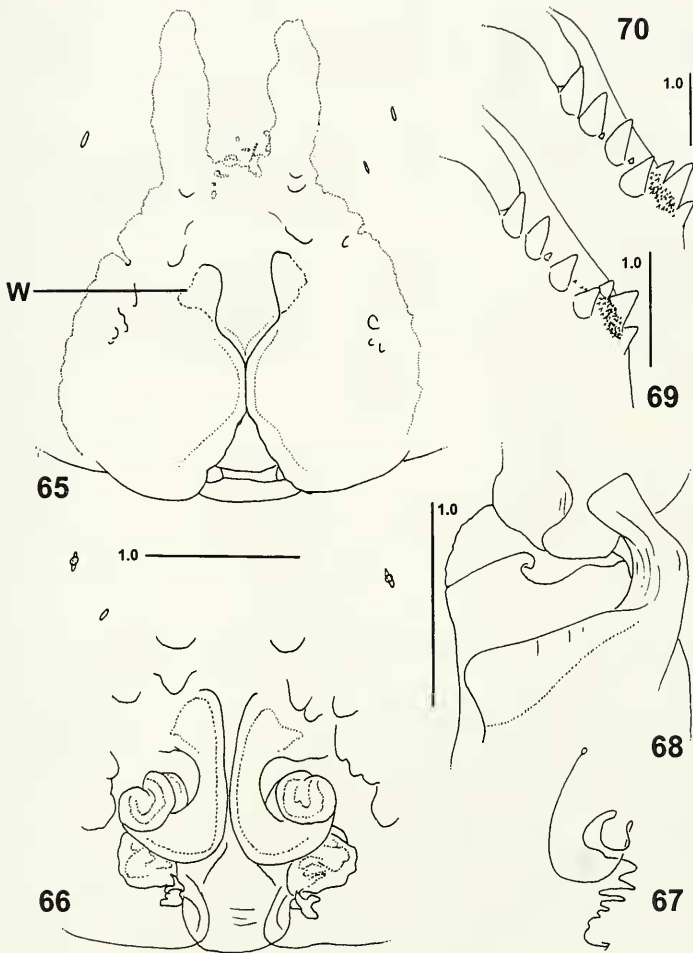
*Note:* One of the legs patellae carries one dorsal spine. This is here recorded for the first time for the whole Sparassidae. However, it could be due to a deformity in ontogeny.

***Heteropoda beroni* sp. n.**

Figs 59-81

*Material examined.* ♂ holotype (PJ 1796): Indonesia, South Sulawesi (= Sulawesi Selatan), Karst Maros, Pangkajene, Gua (=Cave) Mattampa Bawah, 16.iv.2002, Yayuk & Cajyo, Maros Project ARBC-LIPI. (SMF). 1 ♀ paratype (PJ 1797), 1 juvenile ♀ (PJ 1884) with same data as for holotype (MZBI). 2 ♀ paratypes (PJ 1794, 1790): Gua S.1 Balangajea, 28.iv.2002, Yayuk & Cajyo, Maros Project ARBC-LIPI, Aran.2002.0007, Aran.2002.0008 (MZBI). 1 ♀ paratype (PJ 1793): Gua Mimpi, 22.iv.2002, Yayuk & Cajyo, Maros Project ARBC-LIPI, Aran.2002.0009 (MZBI). 1 ♀ paratype (PJ 1789): Gua Mimpi, 22.iv.2002, Yayuk & Cajyo, Maros Project ARBC-LIPI, Aran.2002.0003 (MHNG). 1 ♀, 2 juv. paratypes (PJ 1792, PJ 1885-1886): Gua Rumbia, 21.iv.2002, Yayuk & Cajyo, Maros Project ARBC-LIPI, Aran.2002.0014, Aran.2002.0015-16 (MZBI). 1 ♀ paratype (PJ 1791): Gua Pattunuang, 23.iv.2002, Yayuk & Cajyo, Maros Project ARBC-LIPI, Aran.2002.0006 (MZBI). 1 ♀ paratype (PJ 1795): Gua Saripa, 18.iv.2002, Yayuk & Cajyo, Maros Project ARBC-LIPI, Aran.2002.0005 (MZBI). 1 subadult ♂: Bone, Kahu, Gua Sanggaleri, 20.vii.2001, L. Deharveng & R. Cahyo, Maros Project ARBC-LIPI, Aran.2001.0116. 1 juvenile: Bone, Kahu, Gua Batih, 20.vii.2001, R. Cahyo, Maros Project ARBC-LIPI, Aran.2001.0117. 2 ♀ paratypes (PJ 1206, 1207): Bantimurung, v. Lembatorang the dry cave Lembatorang, 2.ix.1995, P. Beron et T. Ivanova leg. (ZMS). 1 ♀ paratype (PJ 1760): Bantimurung, Gua Balantajia, 4.ix.1995, P. Beron et T. Ivanova leg. (ZMS). 1 ♀ paratype (PJ 1761). 1 juvenile (PJ 1762): Bantimurung, Gua Mimpi, 3.ix.1995, P. Beron et T. Ivanova leg. (SMF).



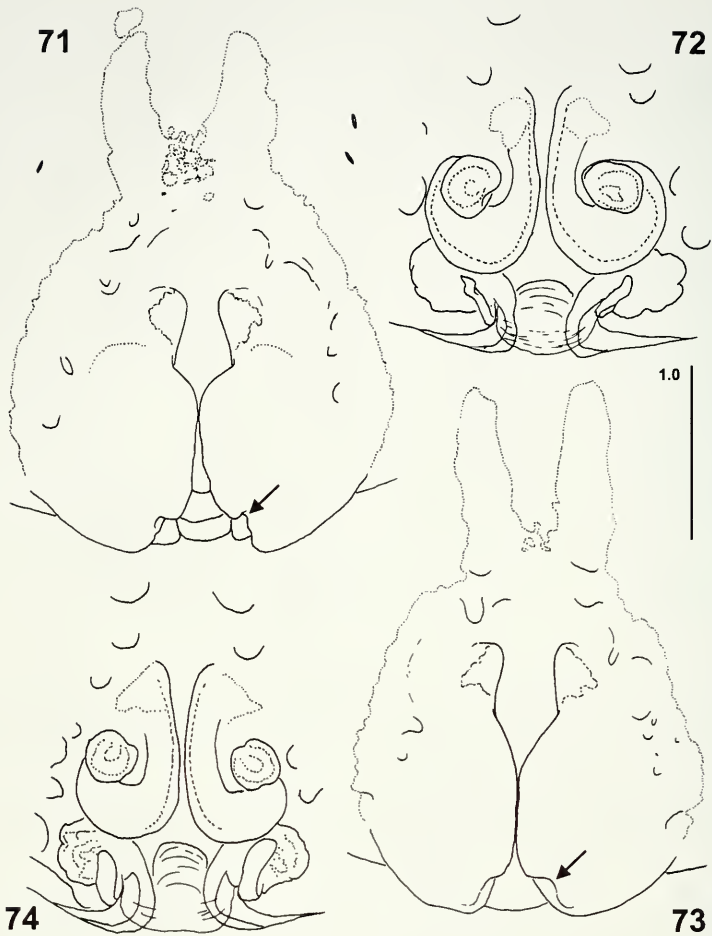


FIGS 65-70

*Heteropoda beroni* sp. n., ♂ holotype (68-69), 1 ♀ paratype from Pangkajene, PJ 1797 (65-67, 70). – Epigyne, ventral view (65); internal genital duct system, dorsal view (66); schematic course of internal genital duct system, dorsal view (67). RTA, retrolateral view (68); furrow of right chelicerae, ventral view (69-70). W = window, close to anterior median septum.

*Etymology*: The specific name is a patronym in honour of one of the collectors, Prof. Petar Beron, and in respect of his efforts in exploring the caves of Asia; noun in genitive case.

*Diagnosis*: The species seems to be related to several forms from Sulawesi and may be recognized by its large size and by the following combination of characters (Figs 59-63, 65-68, 71-74, 80-81): ♂♂: 1. Cymbium elongated, 2. Conductor narrow and its margin straight, i.e. not sigmoid, 3. Tip of RTA in prolatero-dorsal view with sharp edge. ♀♀: 1. Epigyneal field at its posterior lateral margins bent mediad, 2.

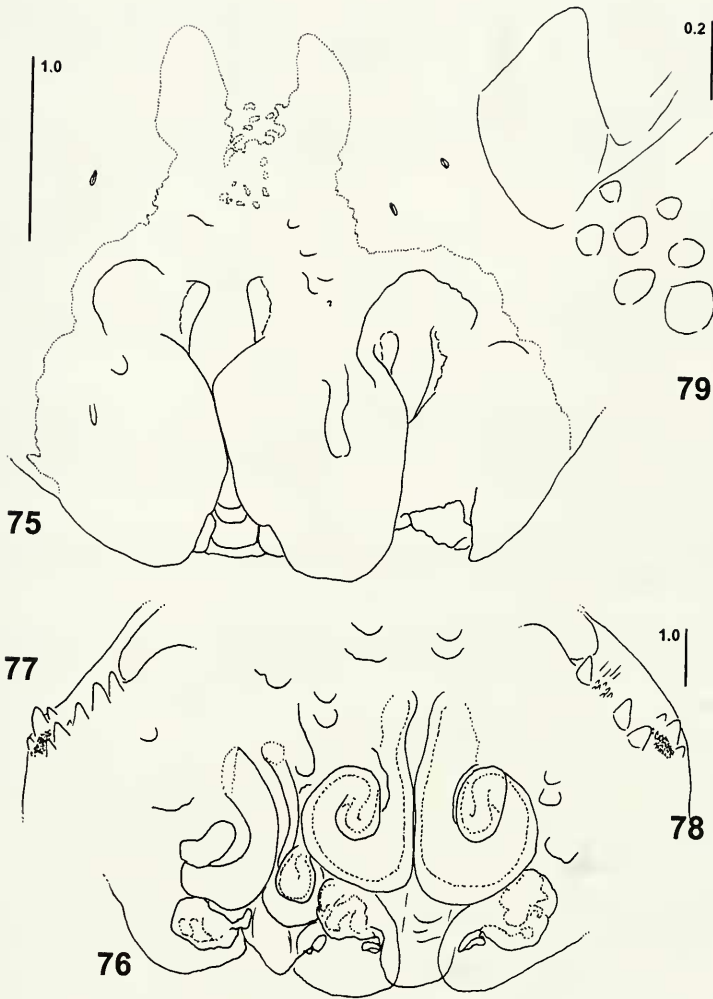


FIGS 71-74

*Heteropoda beroni* sp. n., 2 ♀ paratypes from Bantimurung, PJ 1761 (71-72), PJ 1206 (73-74). – Epigyne, ventral view (71, 73); internal genital duct system, dorsal view (72, 74). Arrows pointing to incision on posterior margin.

Anterior bands half as long as the epigyneal field, 3. Lateral lobes of epigyne touching each other, 4. Margins of median septum anteriorly converging, 5. Posterior part of first winding of internal genital duct system wide, 6. Looped apex spherical, situated at the margin of the first winding, 7. Anterior part of first winding only slightly diverging, directed orad (see arrows in Fig. 80; compare with *H. kuekenthali*, see arrows in Fig. 86).

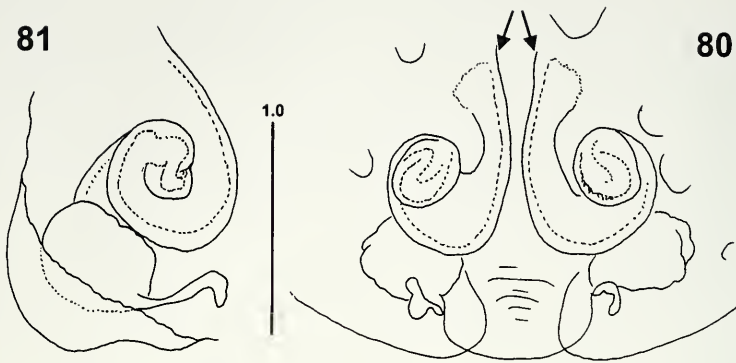
*Description:* ♂ PL 11.6, PW 10.6, AW 5.2, PH 2.8, OL 11.5, OW 6.1. Eyes: AME 0.50, ALE 0.83, PME 0.66, PLE 0.87, AME-AME 0.22, AME-ALE 0.03, PME-PME 0.39, PME-PLE 0.56, AME-PME 0.54, ALE-PLE 0.55, CH AME 0.84, CH ALE 0.55.



FIGS 75-79

*Heteropoda beroni* sp. n., ♀ paratype from Simbang, PJ 1795. – Double epigyne, ventral view (75); double internal genital duct system, dorsal view (76); cheliceral furrow, ventral view, left (77), right (78), detail from 78, showing replacement of a retromarginal tooth by larger denticles (79).

Leg formula: 2143; spination: PP 131, 101, 2121; FE I-II 323, III 333, IV 331; PA 101; TI I-II 2226, III-IV 2126; MT I-II 1014, III 2014, IV 3036. Measurements of palps and legs: PP 20.9 (7.1, 2.9, 4.6, -, 6.3), I 82.6 (21.5, 7.1, 25.1, 23.5, 5.4), II 91.7 (24.0, 7.5, 28.1, 26.6, 5.5), III 68.4 (18.9, 6.2, 21.3, 17.8, 4.2), IV 73.8 (20.3, 6.0, 21.8, 21.4, 4.3). Cheliceral furrow with 3 promarginal and 4 retromarginal teeth. One additional small retromarginal tooth present on the right chelicerae between second and third tooth (Fig. 69).



FIGS 80-81

*Heteropoda beroni* sp. n., ♀ paratype from Bantimurung, PJ 1789. – Internal genital duct system, dorsal view (80), lateral view (81). Arrows pointing to quasi-parallel anterior parts of the internal genital duct system.

Embolus arising from tegulum at 4.30 o'clock, conductor at 10 o'clock. Sperm duct slightly sigmoid (Figs 59, 61). Ventral RTA with straight margin in lateral view (Fig. 60).

Colour: Light reddish brown, almost without pattern. Chelicerae darker brown. DS and legs light reddish brown, with only indistinct spine patches or annulations. Gnathocoxae and labium light red-brown with distal tip yellowish brown. OS lighter reddish brown and almost without markings.

♀ PL 14.1-18.5, PW 12.5-16.2, AW 6.8-9.4, PH 3.6-5.0, OL 16.5-24.8, OW 9.6-15.7. Eyes: AME 0.64-0.71, ALE 1.01-1.02, PME 0.83, PLE 0.98-1.05, AME-AME 0.31-0.36, AME-ALE 0.07-0.15, PME-PME 0.59-0.63, PME-PLE 0.86-0.94, AME-PME 0.70-0.76, ALE-PLE 0.85-0.96, CH AME 1.50-1.53, CH ALE 1.12-1.30.

Leg formula: 2143; spination: PP 131, 101, 2121, 1014; FE I-II, III 32(3)3, IV 331; PA I-III 000(101), IV 101; TI I-II 2026(2226), III-IV 2126(2226); MT I-II 1014, III 2014, IV 3036. Palpal claw with 7-9 teeth. Measurements of palps and legs: PP 28.0-30.2 (8.8-9.2, 4.1-4.2, 6.2-7.1, -, 8.9-9.7), I 84.6-96.5 (22.4-25.3, 9.2-10.2, 25.4-27.8, 22.6-26.0, 5.0-7.2), II 91.8-104.0 (25.1-28.4, 9.8-11.0, 27.5-30.5, 24.3-28.5, 5.1-5.6), III 76.2-84.4 (21.4-24.3, 8.2-9.3, 23.0-24.3, 19.3-21.7, 4.3-4.8), IV 83.4-89.5 (23.0-24.7, 7.9-8.6, 24.1-25.7, 23.4-25.2, 5.0-5.3). Cheliceral furrow with 3 promarginal and 4 retromarginal teeth. Two additional small retromarginal teeth present on the right chelicerae, one between the first and the second, another between the second and the third tooth (Fig. 70).

Epigyne with rounded epigyneal field, distinct anterior bands and bright triangle-shaped 'windows' near the anterior median septum (Fig. 65). Posterior margin of lateral lobes with median incision (see arrows in Figs 71, 73).

Colour: Reddish brown almost without pattern. Chelicerae black. DS and legs reddish brown with only slight spine patches or annulations. Gnathocoxae and labium dark red-brown with distal tip yellowish brown. OS lighter reddish brown and almost without markings.



Variation and deformations: On the chelicerae of one ♀ (PJ 1797) two small additional retromarginal teeth are present (Fig. 77). In one ♀ (PJ 1795) one retromarginal tooth is replaced by larger denticles (Figs 78-79). One ♀ (PJ 1791) possesses a double epigyne and a double internal genital duct system (Figs 75-76). A smaller epigyne is situated on the left side of the normal-sized quasi-central epigyne.

*Distribution:* Indonesia, S-Sulawesi: caves near Maros, Pangkajene, and Bone (Fig. 1: 12-14).

*Biology:* The spiders were sitting on walls inside the cave, facing downwards. Gua Mimpí and Gua Balangajea are deep and wet caves.

*Notes:* According to our present knowledge, *H. beroni* sp. n. groups together with *H. bonthainensis* Merian, 1911 and other species from Sulawesi, some of which were illustrated by Jäger (2002). In order to facilitate a comparison two additional species are illustrated here, which either occur in Sulawesi as well (*H. nigriventer*) or apparently belong to the same phylogenetic lineage (*H. kuekenthali*). A good diagnostic character for this lineage seems to be the course of the internal duct system of ♀ genitalia: The plane of the first winding is directed parallel to the longitudinal axis of the body. The looped apex may be situated in the centre of the first winding or at its margin. The lateral lobes of the epigyne touch each other at one point or along a short distance. In males, known from two species, the tip of the dorsal RTA is widened in retrolateral view (Fig. 68, compare with other *Heteropoda* spp. e.g., Figs 30, 34, 47, 51). More species are needed to establish a diagnosis for a formal species group.

***Heteropoda nigriventer* Pocock, 1897**

Figs 82-84

*Heteropoda nigriventer* Pocock, 1897: 617, pl. 26, fig. 20.

*Material examined:* ♀ holotype (PJ 1763; pinned specimen, formerly dry and recently transferred to alcohol): Indonesia, Sulawesi, Donggala, W. Kükenthal, 97.11.1.122. (NHM).

*Diagnosis:* Epigyneal field with only short and stout anterior bands. Median septum freely visible (Fig. 82). Posterior spermathecae covering parts of the first winding of the internal genital duct system in dorsal view (Fig. 83).

*Description:* PL 10.6, OL 13.7. For further details see Pocock (1897).

*Distribution:* Known only from the type locality (Fig. 1: 15).

***Heteropoda kuekenthali* Pocock, 1897**

Figs 85-90

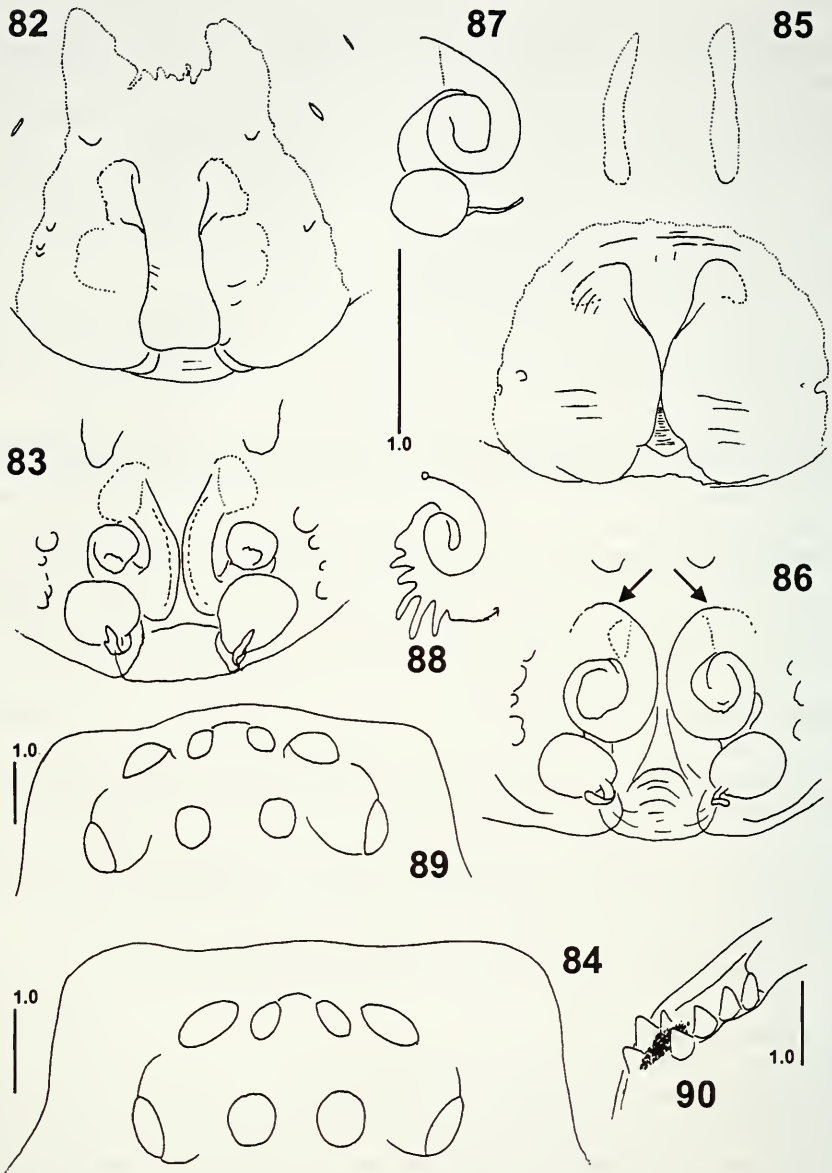
*Heteropoda kuekenthali* Pocock, 1897: 615, pl. 25, fig. 19.

*Material examined:* ♀ holotype (PJ 1764): Indonesia, Halmahera, Soa Kanorra (= Soakonora), 1897.11.1.121. (NHM).

*Diagnosis:* Epigyneal field with long anterior bands, i.e. two third of the length of the field, these separated from the field. Lateral lobes touching each other, their inner margins diverging in their anterior and posterior part (Fig. 85). Spermathecae appearing as round structures in dorsal view, without any overlap with the first winding of the genital duct in dorsal view. Looped apex situated almost in the centre of the first winding. Anterior part of the first winding more strongly bent than in *H. beroni* sp. n., directed laterad (see arrows in Fig. 86).

*Description:* PL 12.3, OL 14.9. For further details see Pocock (1897).

*Distribution:* Known only from the type locality (Fig. 1: 16).



FIGS 82-90

*Heteropoda nigriventer* Pocock. ♀ holotype (82-84), *Heteropoda kuekenthalii* Pocock ♀ holotype (85-90). – Epigyne, ventral view (82, 85); internal genital duct system, dorsal view (83, 86), lateral view (87); schematic course of internal genital duct system, lateral view (88); eye group, dorsal view (84, 89); furrow of left chelicera, ventral view (90). Arrows pointing to the distinctly bent anterior part of the internal genital duct system.

*Heteropoda belua* sp. n.

Figs 91-101

*Material examined:* ♂ holotype (PJ 1736), 2 ♀ paratypes (PJ 1737, 1738): Malaysia, Sarawak, Bau, G. Jambusan, Niang Cave, 26. Chapman, 21.xi.1980 (NHM).

*Etymology:* The specific name refers to the epigyne, which resembles the face of a monster, and the possibility that the cave could be full of these large-sized spiders, which are regarded as 'monsters' with their eyes shining in the light of a torch (Latin: *belua* – monster, beast); noun in apposition.

*Diagnosis:* ♂ ♂ with a distinct process at the base of the embolus (Figs 91, 93). Dorsal RTA with two processes, a thin pin-shaped one and a broad one (Fig. 94). Ventral RTA with a small and a large hump in lateral view (Fig. 92). ♀ ♀: Epigyne with tongue-shaped lateral lobes which are extending beyond the epigastric furrow. Lateral lobes in their posterior part with two small cavities (Fig. 96). Internal genital duct system with spermathecae situated posteriorly and close to each other. First windings in an antero-lateral position, looped apex situated at the median margin of the first windings (Figs 97-99).

*Description:* ♂ PL 8.9, PW 7.7, AW 3.7, PH 3.0, OL 9.0, OW 4.7. Eyes: AME 0.41, ALE 0.57, PME 0.45, PLE 0.55, AME-AME 0.25, AME-ALE 0.07, PME-PME 0.31, PME-PL 0.49, AME-PME 0.38, ALE-PL 0.43, CH AME 1.05, CH ALE 0.78.

Leg formula: 2143; spination: PP 131, 101, 2121; FE I 323, II-III 333, IV 331; PA 101; TI I-II 2226, III-IV 2126; MT I-II 1014, III 2024, IV 3036. Measurements of palps and legs: PP 15.8 (5.5, 2.1, 3.0, -, 5.2), I 68.1 (17.5, 5.4, 21.0, 19.7, 4.5), II 78.3 (20.9, 5.5, 24.3, 22.6, 5.0), III 55.3 (15.6, 4.5, 17.0, 14.6, 3.6), IV 66.6. (18.5, 4.6, 19.3, 19.8, 4.4). Cheliceral furrow with 5 posterior teeth and additional single denticles on the distal margin. Leg claw with long and slender primary tooth (Fig. 101).

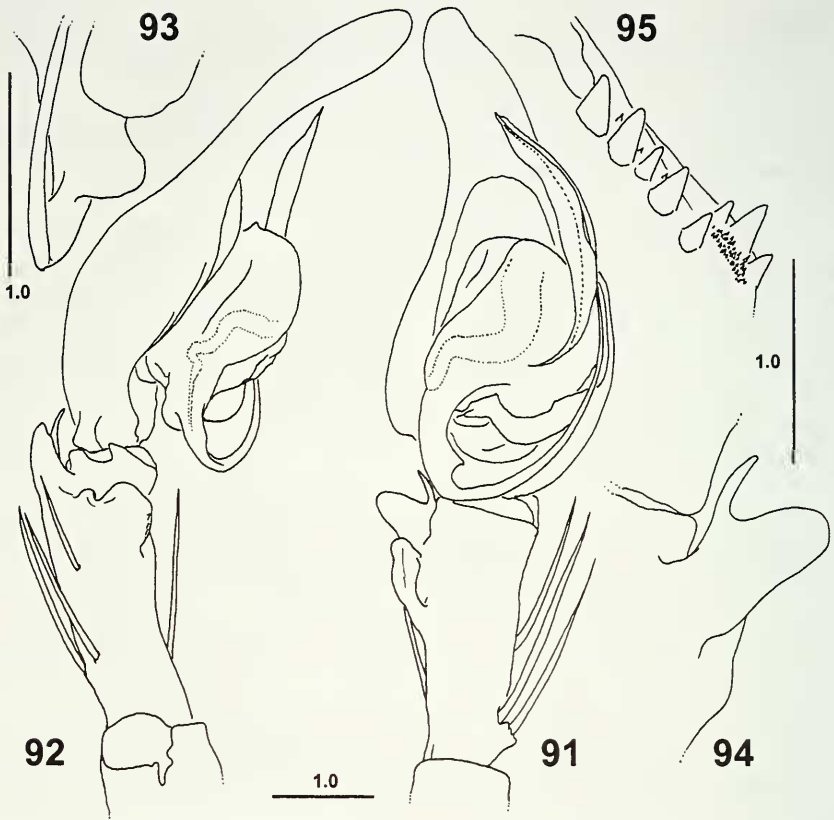
Embolus arising from the tegulum at 3 o'clock, conductor at 9-10 o'clock. Sperm duct wound. Conductor crescent-shaped (Fig. 91). Ventral and dorsal RTA distinctly separated in lateral view (Fig. 92).

Colour: As the ♂ holotype is not well preserved, only recognizable features of colouration are given. Body and legs generally yellowish brown. Chelicerae darker in their basal half. FE and TI slightly annulated.

♀ (measurements of paratypes). PL 14.2-15.2, PW 12.5-13.0, AW 6.4-6.8, PH 4.0-4.2, OL 15.1-16.2, OW 8.4-8.8. Eyes: AME 0.57, ALE 0.80, PME 0.61-0.64, PLE 0.76-0.77, AME-AME 0.45-0.48, AME-ALE 0.17-0.18, PME-PME 0.52-0.55, PME-PL 0.84-0.86, AME-PME 0.67-0.69, ALE-PL 0.68-0.73, CH AME 1.87-1.96, CH ALE 1.51-1.57.

Leg formula: 2413; spination: PP 131, 101, 2121, 1014; FE I 323, II-III 333, IV 331(2); PA 101; TI 2126; MT I-II 1014, III 2014, IV 3036. Palpal claw with 9-11 teeth. Measurements of palps and legs: PP 25.6-27.0 (7.5-8.0, 3.7-3.8, 5.8-6.5, -, 8.6-8.7), I 84.6-85.5 (22.6-23.0, 8.0, 25.7-25.8, 23.1-23.7, 5.1), II 92.9-93.8 (24.9-25.7, 8.2-8.4, 28.3-28.8, 25.4-25.6, 5.5-5.9), III 73.8-73.9 (21.0-21.3, 7.1-7.3, 22.1-22.0, 18.6-19.0, 4.6-4.7), IV 88.5-88.6 (24.4-25.2, 7.1-7.2, 26.0-26.2, 24.6-25.3, 5.5-5.6). Cheliceral furrow with 5-6 posterior teeth and additional single denticles on the distal margin.

Epigyneal field roundish, slightly separated from anterior bands (Fig. 96). First winding of internal genital duct system situated laterally, loops directed mediad (Figs 97-99).



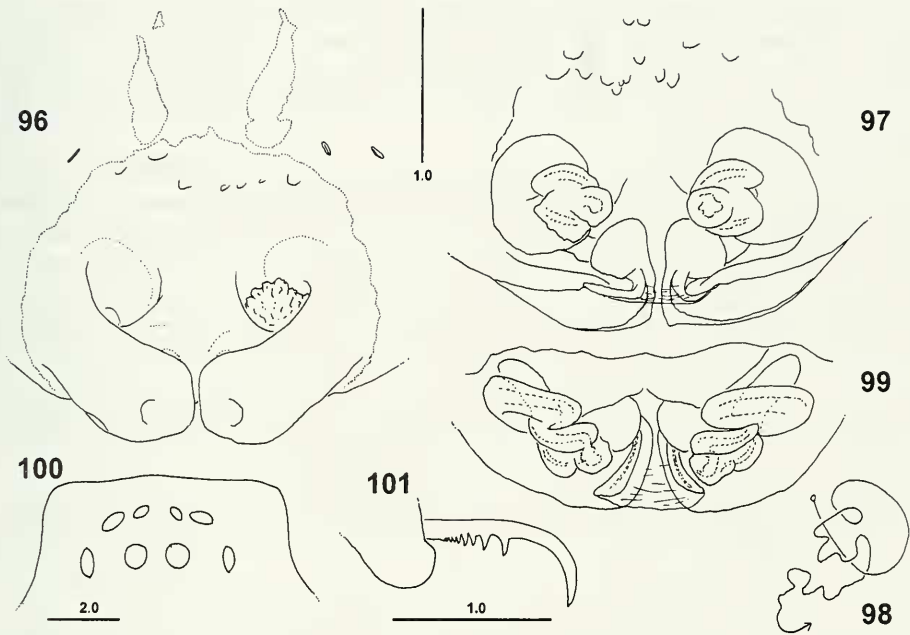
FIGS 91-95

*Heteropoda belua* sp. n., ♂ holotype. – Right palp, slightly expanded, ventral view (91), retrolateral view (92); base of embolus, prolateral view (93); RTA, dorsal view (94); furrow of right chelicera, ventral view (95).

Colour: Reddish brown, almost without distinct markings. Chelicerae dark reddish brown to black. FE with dark spine patches. Distal leg segments darker. DS and dorsal OS covered by short dark hairs.

*Distribution*: Known only from the type locality (Fig. 1: 11).

*Notes*: This species represents another large-sized cave-dwelling *Heteropoda* species. It cannot be grouped together with any other known species. Although the ♂ holotype is distinctly smaller than the ♀ paratypes, all three specimens are considered conspecific. This assumption is supported by the congruence of apomorphic characters as e.g. additional retromarginal cheliceral teeth and additional single denticles on the distal margin of the cheliceral furrow. From Australian *Heteropoda* species it is also known that ♂♂ may vary greatly in size (Davies 1994). This is confirmed by specimens of *Heteropoda maxima* (personal observations in Laotian caves) and of *Heteropoda beroni* sp. n. (this paper).



FIGS 96-101

*Heteropoda belua* sp. n., ♂ holotype (101), ♀ paratype, PJ 1737 (96-100). – Epigyne, ventral view (96); internal genital duct system, dorsal view (97), anterior view (99); schematic course of internal genital duct system, dorsal view (98); eye group, dorsal view (100); prolateral claw of leg IV, prolateral view (101).

## DISCUSSION

It is astonishing that the largest labidognathous spiders – according to leg span (20-30 cm) and to body length (3-5 cm) – have become known just recently (Jäger, 2001a: *Heteropoda maxima*; this paper). All these species are known from cave habitats, which could be one reason for their late discovery. At present these large to very large species are known from North India (Meghalaya: *H. robusta* Fage, *H. fischeri* sp. n.), Thailand (*H. schwendingeri* sp. n.), Laos (*H. maxima*), Borneo (*H. belua* sp. n.) and Sulawesi (*H. beroni* sp. n.).

With regard to phylogenetic relationships among *Heteropoda* species, the genus is far from being well investigated. Although the sexual dimorphism of elongated hairs on metatarsi in male *Heteropoda* specimens seems to be more distinct in cave-dwelling species, it is not suitable for tracing phylogenetic relationships, as it occurs in several genera of Heteropodinae in cave-dwellers as well as in non-cave-dwellers. Moreover this kind of sexual dimorphism is known from other spider families e.g., Lycosidae: *Pardosa purbeckensis* O.F. Pickard-Cambridge, 1895, *Pardosa plumipes* (Thorell, 1875) (Tongiorgi, 1966). As the elongated metatarsal hairs occur exclusively in adult males, this morphological structure could be linked to sexual behaviour during the mating procedure.



Another trait, which is seen in all mentioned cave-dwelling *Heteropoda* species, is the presence of elongated appendages, especially pronounced in the male cymbium. This is known as troglobiomorphism and occurs also in other spider families e.g., Linyphiidae, Theridiidae (Ruzicka, 1998) and Agelenidae (Roth, 1968: *Tegenaria mexicana mexicana* Roth).

Relationships between the species described in the present paper can be best traced on the basis of the genitalia. In *H. fischeri* sp. n. the affiliation to the group which includes *H. robusta* and *H. afghana* is apparent from the striking similarities in the female copulatory duct system. All three species were found in cave habitats. All localities are located in a marginal zone of the distributional range of *Heteropoda* Latreille (Jäger, 2001b: fig. 63) and representatives of Heteropodinae are generally found in humid habitats as forests, leaf litter, rock crevices etc. Therefore the occurrence of *H. afghana* in caves only is probably due to less rainfall in this region. This seems to be true also for another species, *Heteropoda variegata* (Simon, 1871) from the eastern Mediterranean region, which exclusively inhabits caves and cave-like habitats (Levy, 1989). However, from the isolated distributional range of the latter species it remains unclear whether it has been introduced to this region or should be considered as a relict.

Some specimens show an unusually high variation of their genitalia and of other characters (body length, leg spination) and are here only tentatively placed close to *H. afghana*. A group of *Pseudopoda* species is known from the western Himalaya, i.e. *P. prompta* (O. Pickard Cambridge, 1882), *P. casaria* (Simon, 1897), *Pseudopoda* sp. cf. *casaria* (Simon, 1897), which also tends to have highly variable genitalia (Jäger, 2001b). In both genera this seems to be the initial phase of isolation of single marginal populations, as proposed by Sedlag (1995: 18), where geographical separation leads to higher variation.

Although all four forms listed above can be clearly grouped together, I avoid to establish new species groups, as relationships to other species with a similar course of the internal duct system and type of winding in female genitalia are not clear (axis of winding parallel to longitudinal axis of the body also occurs in: *H. umbrata* Karsch from Sri Lanka, *H. sexpunctata* Simon from the Himalayas, *H. cyperusiria* Barrion & Litsinger from the Philippines, *Heteropoda* spp. from India, Sri Lanka, Sumatra).

The general type of winding of the female internal genital duct system of *H. beroni* sp. n. is similar to those of several other species, among them *H. maxima* from Laos, *H. strasseni* Strand from Java, *H. kuekenthali* from Halmahera and the above mentioned species from Sulawesi (Jäger, 2002). Since no additional characters are available, no final conclusions on the phylogenetic relationships of these species can be drawn.

*H. schwendingeri* sp. n. seems to be close to *H. tetrica* from Myanmar and northern Thailand. Female *Heteropoda* specimens of the same species group are also known from southern Thailand. Since there are no definite conspecific specimens of the latter forms available, they are not included in this study.

I can conclude that inspite of superficial similarities (large size, elongated appendages, distinctly elongated hairs on male fore-legs) the cave-dwelling species treated here do not seem to be closely related to each other, but to regional species

groups. Thus I assume that species entered the caves independently and that similar characters were acquired secondarily due to similar conditions in the caves.

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